![esa logo]

Promoting the Science of Ecology

Nutrients in Senesced Leaves: Keys to the Search for Potential Resorption and Resorption
Proficiency
Author(s): Keith T. Killingbeck
Reviewed work(s):
Source: *Ecology*, Vol. 77, No. 6 (Sep., 1996), pp. 1716-1727
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/2265777
Accessed: 31/01/2012 03:11

Editor's Note

Because I sincerely doubt that my own opinion about the merits of Killingbeck's contribution to plant physiological ecology would carry much weight with those of you interested in reading his paper, I have instead chosen to quote directly from the manuscript's referees, both of whom have kindly agreed to forgo anonymity.

Nelson G. Hairston, Jr.

"This manuscript introduces the concept of nutrient resorption proficiency (the minimum level to which a plant can reduce an element in senescing leaves), and then asks (i) whether resorption proficiencies are convergent across terrestrial plant species; and (ii) whether resorption proficiencies of N and P are related to leaf duration, N-fixation, and/or each other. Killingbeck answers each of these questions in the affirmative, based on comparative analyses of published data for 89 species of woody perennials" (T. J. Givnish). "Given that the data were obtained from many different species [obtained by] different investigators, . . . the generalities detected are even more remarkable" (T. E. Dawson). "To a certain extent, the concept of resorption proficiency clarifies what had become a confusing welter of data on resorption efficiency (proportion of the original level of a nutrient resorbed before leaf abscission)" (T. J. Givnish).

Thomas J. Givnish
Todd E. Dawson

NUTRIENTS IN SENESCED LEAVES: KEYS TO THE SEARCH FOR POTENTIAL RESORPTION AND RESORPTION PROFICIENCY[1]

KEITH T. KILLINGBECK
*Department of Biological Sciences,
University of Rhode Island, Kingston, Rhode Island 02881 USA*

Abstract

Analyses of nitrogen and phosphorus in the senesced leaves of 89 species of deciduous and evergreen woody perennials were used (1) to discover the limits of ultimate potential resorption (maximal withdrawal of nutrients from senescing leaves), (2) to determine a means by which resorption can be categorized as complete or incomplete, (3) to develop the concept of resorption proficiency (measured as the levels to which nutrients have been reduced in senesced leaves), (4) to compare resorption in evergreen vs. deciduous species, (5) to assess the impact of phylogeny on resorption, (6) to compare resorption in actinorhizal vs. non-nitrogen-fixing species, and (7) to consider the efficacy of using multiple measures of resorption to answer questions regarding the function and evolution of this process, rather than relying solely on analyses of resorption efficiency (percentage reduction of nutrients between green and senesced leaves).

Concentrations of 0.3% nitrogen and 0.01% phosphorus in senesced leaves represent ultimate potential resorption of these nutrients in woody perennials. Resorption proficiency and potential resorption were quantitatively defined in two models that describe both resorption that is maximal and biochemically complete, and that which is not. Resorption is highly proficient in plants that have reduced nitrogen and phosphorus in their senescing leaves to concentrations below 0.7% and 0.05%, respectively. An important feature of knowing the levels to which nutrients can be reduced in senescing leaves is that these values offer an objective

gauge by which to measure the success of resorption as a nutrient conservation mechanism.

Evergreens were significantly more proficient at resorbing phosphorus than were deciduous species (0.045% vs. 0.067% P in senesced leaves, respectively) and plants capable of symbiotic nitrogen fixation were significantly less proficient at resorbing nitrogen than were nonfixers (1.6% vs. 0.9% N in senesced leaves, respectively). Resorption proficiency appeared to parallel some phylogenic trends, yet the influence of phylogeny was not so significant as to overwhelm the effects of recent selection. The ability of plants to reduce nitrogen in senescing leaves was significantly correlated with their ability to reduce phosphorus.

Measurement and analysis of resorption proficiency, when coupled with concurrent consideration of potential resorption and resorption efficiency, should facilitate and expedite the ongoing attempt to resolve complex questions regarding the environmental constraints that influence resorption, and the selection pressures that have directed the evolution of this process.

Key words: deciduous; evergreen; nitrogen; nitrogen fixation; nutrient cycling; phosphorus; potential resorption; realized resorption; resorption efficiency; resorption proficiency; senesced leaves; senescence.

Introduction

The terminal concentrations of phloem-mobile nutrients in senesced leaves are primarily determined by the process of nutrient resorption. This process controls the mobilization and removal of nutrients from senescing plant tissues, and the transport of these nutrients to storage sites in perennial tissues (Chapin 1980, Killingbeck 1986). Resorption is one of the most important of all strategies employed by plants to conserve nutrients and, consequently, influences processes as varied as competition, nutrient uptake, and productivity. Because most organisms are directly or indirectly dependent on the nutrients available in plant tissues deposited as litter, and because falling leaves account for ≈70% of all aboveground litter (O'Neill and DeAngelis 1981), it is clear that resorption is a keystone process in most, if not all, ecosystems.

Our understanding of resorption comes primarily from single-year studies, which implicitly assume that resorption measured once for a given individual or population is a representative, invariant measure of the resorption capacity of that plant or plants. That may be so for some species in some environments, but it is not universally true for the few species in which resorption has specifically been tracked for ≥3 yr. Individual plants and plant populations can resorb markedly different amounts of nutrients in different years (Killingbeck et al. 1990, May and Killingbeck 1992, Killingbeck 1993a), indicating that maximum

resorption (potential resorption) is not always the same as measured resorption (realized resorption; Killingbeck et al. 1990). Apparently, a variety of parameters (e.g., water availability: Hocking 1982, Escudero et al. 1992; timing of abscission: Killingbeck et al. 1990, del Arco et al. 1991; shade: Chapin and Moilanen 1991) may cause realized resorption to be less successful than potential resorption at conserving nutrients in some years.

Consider the example of highly variable realized resorption in the desert shrub, ocotillo (*Fouquieria splendens*). Resorption of nitrogen (N) in a single population of this drought-deciduous desert shrub varied from 11% in 1986 (Killingbeck 1992; a value not statistically different from zero resorption) to 72% in 1989 (Killingbeck 1993b). Interspecific comparisons utilizing 11% as the value representing N resorption in ocotillo would have been completely invalid, yet such comparisons would likely have emerged in the literature were it not for the subsequent measurements of resorption in 1989. If potential resorption could have been measured or estimated in 1986, it would have been clear that realized resorption in that year did not come close to approaching potential resorption.

The fundamental problem imposed by the temporal variability in resorption is that it is virtually impossible to know whether measured differences in resorption efficiencies (percent reduction of a nutrient between green and senesced leaves) among species or among sites are differences in potential resorption, which would have clear evolutionary implications, or merely the vagaries of temporal differences in realized resorption. Our present inability to differentiate between realized and potential resorption continues to hinder efforts to identify selection pressures that have been paramount in determining species-to-species and site-to-site differences in resorption efficiencies. For instance, one of the most perplexing and confounding issues surrounding our understanding of resorption in terrestrial plants is whether or not resorption efficiency is a function of soil fertility. It is intuitively appealing to suggest that resorption efficiency should be high in infertile sites and lower in fertile sites, yet there are copious data (e.g., Small 1972, Stachurski and Zimka 1975, Staaf 1982, Birk and Vitousek 1986, Ralhan and Singh 1987, Chapin and Moilanen 1991) and ardent proponents on both sides of this debate. This problem, among others, will probably remain intractable if realized and potential resorption remain totally indiscriminable.

Although there are no direct measures of potential resorption, estimates of the degree to which realized resorption approaches potential resorption in individual species populations can be achieved by developing

TABLE 1. Concentrations (%) of nitrogen (N) and phosphorus (P) in the senesced leaves of 77 species of woody perennial plants. Overall means of N and P given at the end of the table were calculated by giving each species equal weighting. When multiple records were available for a species, such as *Acer rubrum,* only the mean of the available values for that species was used in calculating the overall mean for all species.

Species	Location	% N	% P	Citation
Deciduous species:				
Acer monospessulanum†	Spain	1.14	0.05	Escudero et al. 1992
Acer rubrum‡	Ohio, USA	0.70	0.07	Boerner 1984
Acer rubrum§	Tennessee, USA	0.49	0.03	Grizzard et al. 1976
Betula alleghaniensis§	New Hampshire, USA	1.17	0.11	Hoyle 1965
Betula papyrifera§	Alaska, USA	0.50	0.10	Chapin and Kedrowski 1983
Betula papyrifera‡	Alaska, USA	0.88	0.14	Chapin and Moilanen 1991
Betula pubescens†	Spain	0.65	0.03	Escudero et al. 1992
Byrsonima crassifolia§	Venezuela	0.57	0.02	Montes and Medina 1977
Carya tomentosa§	Tennessee, USA	0.53	0.03	Grizzard et al. 1976
Celtis occidentalis	Kansas, USA	0.90	0.11	Killingbeck 1984
Clethra alnifolia	Georgia, USA	0.61	0.02	DeLucia and Schlesinger 1995
Crataegus monogyna†	Spain	1.02	0.09	Escudero et al. 1992
Curatella americana§	Venezuela	0.46	0.01	Montes and Medina 1977
Fagus grandifolia‡	Ohio, USA	0.82	0.06	Boerner 1984
Fagus sylvatica§	Germany	1.06	0.07	Olsen 1948
Fagus sylvatica¶	Sweden	1.15	0.08	Staaf and Stjernquist 1986
Fouquieria splendens	New Mexico, USA	1.20	⋯	Killingbeck 1992
Fouquieria splendens	New Mexico, USA	0.60	0.02	Killingbeck 1993b
Frangula alnus†	Spain	1.13	0.03	Escudero et al. 1992
Fraxinus angustifolia†	Spain	1.39	0.09	Escudero et al. 1992
Fraxinus pensylvanica	Kansas, USA	1.00	0.14	Killingbeck 1984
Genipa caruto§	Venezuela	0.97	0.05	Montes and Medina 1977
Godmania macrocarpa§	Venezuela	0.77	0.03	Montes and Medina 1977
Itea virginica	Georgia, USA	0.57	0.02	DeLucia and Schlesinger 1995
Larix laricina§	Alaska, USA	0.47	0.12	Chapin and Kedrowski 1983
Larix laricina§	Minnesota, USA	0.45	0.17	Tilton 1977
Larix laricina#	Wisconsin, USA	0.85	0.04	Tyrell and Boerner 1987
Leucothoe racemosa	Georgia, USA	0.55	0.01	DeLucia and Schlesinger 1995
Liriodendron tulipifera§	Tennessee, USA	1.14	0.04	Grizzard et al. 1976
Luehea candida§	Venezuela	0.99	0.08	Montes and Medina 1977
Nyssa sylvatica§	Tennessee, USA	0.53	0.04	Grizzard et al. 1976
Oxydendrum arboreum§	Tennessee, USA	0.87	0.09	Grizzard et al. 1976
Populus deltoides§	Mississippi, USA	0.68	0.02	Baker and Blackmon 1977
Populus nigra†	Spain	0.67	0.04	Escudero et al. 1992
Populus tremuloides††	Rhode Island, USA	0.70	0.04	Killingbeck et al. 1990
Populus tremuloides§	Minnesota, USA	0.74	0.10	Verry and Timmons 1976
Prunus spinosa†	Spain	1.57	0.09	Escudero et al. 1992
Pyrus bourgaeana†	Spain	0.88	0.06	Escudero et al. 1992
Quercus alba‡	Ohio, USA	0.60	0.05	Boerner 1984
Quercus alba§	Tennessee, USA	1.23	0.08	Grizzard et al. 1976
Quercus alba§	New York, USA	0.51	0.03	Woodwell 1974
Quercus coccinea§	New York, USA	0.45	0.01	Woodwell 1974
Quercus faginea†	Spain	1.05	0.07	Escudero et al. 1992
Quercus macrocarpa	Kansas, USA	1.00	0.14	Killingbeck 1984
Quercus muhlenbergii	Kansas, USA	1.00	0.15	Killingbeck 1984
Quercus prinus‡	Ohio, USA	0.74	0.05	Boerner 1984
Quercus prinus§	Tennessee, USA	0.79	0.03	Grizzard et al. 1976
Quercus pyrenaica†	Spain	0.98	0.06	Escudero et al. 1992
Quercus rubra§	Tennessee, USA	1.09	0.07	Grizzard et al. 1976
Salix atrocinerea†	Spain	1.13	0.09	Escudero et al. 1992
Sambucus nigra†	Spain	1.90	0.21	Escudero et al. 1992
Symplocos ramosissima‖	India	1.80	0.03	Ralhan and Singh 1987
Taxodium distichum	Florida, USA	0.84	0.05	Dierberg et al. 1986
Ulmus rubra	Kansas, USA	1.40	0.16	Killingbeck 1984
Viburnum cotinifolium‖	India	1.50	0.10	Ralhan and Singh 1987
Evergreen species:				
Banksia grandis	Australia	0.26	0.01	O'Connell et al. 1978
Brosimum lactescens	Brazil	1.30	0.05	Scott et al. 1992
Cistus monspeliensis	Spain	1.07	0.08	Jonasson 1989
Cyrilla racemiflora	Georgia, USA	0.38	0.01	DeLucia and Schlesinger 1995

TABLE 1. Continued.

Species	Location	% N	% P	Citation
Duguetia lucida	Brazil	1.64	0.06	Scott et al. 1992
Eucalyptus calophylla	Australia	0.30	0.01	O'Connell et al. 1978
Eucalyptus diversicolor‡	Australia	0.49	0.02	O'Connell and Menagé 1982
Eucalyptus marginata	Australia	0.30	0.01	O'Connell et al. 1978
Eucalyptus ragnans‡	Australia	0.67	0.03	Polglase and Attiwill 1992
Ilex aquifolium†	Spain	0.70	0.03	Escudero et al. 1992
Lecythis corrugata	Brazil	1.13	0.06	Scott et al. 1992
Licania kunthiana	Brazil	1.23	0.05	Scott et al. 1992
Lyonia lucida	Georgia, USA	0.32	0.01	DeLucia and Schlesinger 1995
Nothofagus truncata§	New Zealand	1.11	0.10	Miller 1963
Picea mariana‖	Wisconsin, USA	0.42	0.03	Tyrrell and Boerner 1987
Pinus echinata§	Tennessee, USA	0.51	0.04	Grizzard et al. 1976
Pinus halepensis†	Spain	0.62	0.03	Escudero et al. 1992
Pinus pinaster†	Spain	0.55	0.04	Escudero et al. 1992
Pinus pinea†	Spain	0.66	0.06	Escudero et al. 1992
Pinus rigida§	New York, USA	0.34	0.01	Woodwell 1974
Pinus roxburghii‖	India	1.00	0.09	Ralhan and Singh 1987
Pinus sylvestris†	Spain	0.52	0.04	Escudero et al. 1992
Pinus sylvestris‖	Sweden	0.50	···	Näsholm 1994
Pinus taeda§	Tennessee, USA	0.68	0.04	Grizzard et al. 1976
Pouteria hispida	Brazil	1.17	0.04	Scott et al. 1992
Pseudotsuga menziesii§	Washington, USA	0.57	···	Turner and Olson 1976
Quercus coccifera§	Spain	0.82	0.03	Escudero et al. 1992
Quercus leucotrichophora‖	India	1.50	0.11	Ralhan and Singh 1987
Quercus rotundifolia†	Spain	0.87	0.05	Escudero et al. 1992
Quercus suber†	Spain	0.87	0.06	Escudero et al. 1992
Shorea robusta‖	India	1.30	0.10	Ralhan and Singh 1987
Taxus baccata†	Spain	0.81	0.07	Escudero et al. 1992
Tetragastris panamensis	Brazil	0.89	0.04	Scott et al. 1992
Mean (all species)		0.87	0.06	
Standard error of the mean		0.04	0.01	

† Concentrations calculated from N and P resorption efficiencies and concentrations in green leaves.
‡ Lowest N and P values among multiple sites.
§ Calculated from data in Chapin and Kedrowski (1983: Table 1).
‖ Interpolated from a figure in the citation.
¶ Mean of high and low crown leaves.
# P concentration interpolated from a figure in the citation.
†† Lowest N and P values among multiple years.

a detailed knowledge of the levels to which species can reduce nutrients in their senescing leaves (resorption proficiency). Toward that end, the overall objective of this paper is to utilize the extant literature to quantify potential resorption in terms of terminal N and phosphorus (P) levels in senesced leaves.

The specific goals of this paper are to (1) determine the levels to which woody perennial plants can reduce N and P in senescing leaves; (2) search for minima below which further reductions of N and P in senescing leaves are unlikely, or biochemically impossible (i.e., ultimate potential resorption); (3) establish benchmark levels of N and P in senesced leaves that define complete and incomplete resorption; (4) compare the abilities of evergreen and deciduous plants to reduce N and P in senescing leaves; (5) explore the potential impact of phylogeny on resorption proficiency; (6) compare the abilities of species with, and without, nitrogen-fixing symbionts to reduce N and P in se-

nescing leaves; and (7) examine the possibility that the ability of plants to reduce N in senescing leaves is correlated with their ability to reduce P in senescing leaves.

Methods

The database for this analysis is a compilation of values for N and/or P in the senesced leaves of 89 species of woody perennial plants. Data were gleaned from the literature in the following way. The initial synthesis was assembled from a summary table of resorption efficiency values published by Chapin and Kedrowski (1983: Table 1). Nitrogen and/or P concentrations in senesced leaves were calculated for species in which both green-leaf nutrient concentration and resorption efficiency were reported.

Data for the remaining 62 species were taken from papers published after 1983, in which resorption dynamics were considered and concentrations (percent

TABLE 2. Concentrations (%) of nitrogen (N) and phosphorus (P) in the senesced leaves of woody perennial plants from genera known to be actinorhizal (nitrogen-fixing symbiont = *Frankia*).

Species	Location	% N	% P	Citation
Alnus crispa†	Alaska, USA	0.94	0.02	Chapin and Kedrowski 1983
Alnus glutinosa	Spain	2.30	0.10	Rodríguez-Barrueco et al. 1984
Comptonia peregrina	Rhode Island, USA	1.80	0.04	Killingbeck 1993a
Elaeagnus umbellata‡,§	Illinois, USA	2.30	⋯	Côté et al. 1989
Casuarina decussata	Australia	0.42	0.01	O'Connell and Menagé 1982
Myrica esculenta‡	India	1.90	0.05	Ralhan and Singh 1987
Mean (all species)		1.61	0.04	
Standard error of the mean		0.31	0.02	

† Calculated from data in Chapin and Kedrowski (1983: Table 1).
‡ Interpolated from a figure in the citation.
§ Prairie site only.

of dry leaf mass) or absolute contents (micrograms per square centimetre of leaf surface) of N and/or P were provided for senesced leaves (or data sufficient for calculating these values). Species were rejected if they had been experimentally manipulated in any way, or were growing in environments other than natural ecosystems (e.g., plantations, lawns).

After the assembled data were examined, it appeared that data on P from Fries (1952), reported accurately by Chapin and Kedrowski (1983) from the original 1952 paper, were flawed. Of seven reported values >0.20% P in my original compilation, six came from Fries (1952). Further, Fries (1952) reported P concentrations almost double (0.39% P) that of the next highest "non-Fries" value (0.21% P). In the two species from which P concentrations were reported both by Fries and another author (*Betula pubescens, Fagus sylvatica*), values reported by Fries were 566% and 73% higher than the values reported by other authors. Therefore, the data from Fries (1952) were eliminated from this analysis.

In the penultimate compilation, species in genera known to contain nitrogen-fixing symbionts were removed and placed in Table 2. All such species were actinorhizal (nonleguminous plants harboring the nitrogen-fixing symbiont *Frankia*; Baker and Schwintzer 1990). The remaining species were segregated into deciduous and evergreen species.

During the literature search, 22 species were found in which absolute N and P contents in senesced leaves were available (i.e., per unit area content, micrograms per square centimetre). These data were compiled in Table 3.

Species nomenclature was taken directly from the cited papers; no attempt was made to adjust names to fit recent taxonomic changes. Taxonomic classification for purposes of phylogenetic comparisons within the division Anthophyta followed Cronquist (1988).

Statistical analyses were performed with SYSTAT software (Wilkinson 1992). Normality of data distribution was determined with the Lilliefors' test. Means were compared with parametric statistics (Student's *t* test, ANOVA, Fisher's least significant difference [LSD] test) when the assumption of normality was met, and with nonparametric, distribution-free statistics (Kruskal-Wallis, Mann-Whitney *U* test) when data were not normally distributed. Correlation analyses were generated with the Pearson product–moment correlation statistic.

Results

Nitrogen concentration in the senesced leaves of 77 species of deciduous and evergreen woody perennials varied from 0.26% in *Banksia grandis* growing in Australia, to 1.90% in *Sambucus nigra* growing in Spain (Table 1). Mean N concentration in the senesced leaves of the same 77 species was 0.87%. Phosphorus concentration in the senesced leaves of 76 species ranged from 0.01% in nine species growing in Australia, the USA, and Venezuela, to 0.21% in *Sambucus nigra* growing in Spain (Table 1). Mean P concentration in the senesced leaves of these species was 0.06%.

Considered separately, the deciduous and evergreen species produced senesced foliage that held similar amounts of N but different amounts of P (Fig. 1). Evergreens were capable of reducing P in their senesced foliage to much lower concentrations (0.045%) than were deciduous plants (0.067%). Additionally, the highest P concentration in the senesced leaves of evergreens (0.11%, *Quercus leucotrichophora*) was only half that of the highest P concentration among deciduous species (0.21%, *Sambucus nigra*).

Concentrations of N and/or P in senesced leaves of the eight genera for which there were three or more observations in Table 1 (*Acer, Betula, Eucalyptus, Fagus, Larix, Populus, Quercus, Pinus*) varied among taxonomic divisions (Coniferophyta vs. Anthophyta: $P < 0.05$ for N, ANOVA; $P > 0.05$ for P, Kruskal-

TABLE 3.   Content ($\mu g/cm^2$) of nitrogen (N) and phosphorus (P) in the senesced leaves of 22 species of woody perennial plants. All species are deciduous except *Cistus monspeliensis, Cyrilla racemiflora,* and *Lyonia lucida.* Overall means of N and P given at the end of the table were calculated by giving each species equal weighting.

Species	Location	N	P	Citation
Betula papyrifera†	Alaska, USA	36	7.8	Chapin and Moilanen 1991
Celtis occidentalis	Kansas, USA	60	7.0	Killingbeck 1984
Cistus monspeliensis	Spain	128	9.3	Jonasson 1989
Clethra alnifolia	Georgia, USA	60	1.8	DeLucia and Schlesinger 1995
Comptonia peregrina¶	Rhode Island, USA	142	2.6	Killingbeck 1993
Cyrilla racemiflora	Georgia, USA	39	0.3	DeLucia and Schlesinger 1995
Fagus sylvatica‡,§	Sweden	46	3.1	Staaf and Stjernquist 1986
Fouquieria splendens	New Mexico, USA	128	9.0	Killingbeck 1992
Fraxinus pensylvanica	Kansas, USA	75	11.0	Killingbeck 1984
Gaylussacia baccata	Rhode Island, USA	43	3.6	Killingbeck and Costigan 1988
Hamamelis virginiana‡	Ohio, USA	22	2.7	Boerner 1985
Itea virginica	Georgia, USA	47	1.8	DeLucia and Schlesinger 1995
Leucothoe racemosa	Georgia, USA	50	1.0	DeLucia and Schlesinger 1995
Lyonia lucida	Georgia, USA	74	1.4	DeLucia and Schlesinger 1995
Populus tremuloides‖	Rhode Island, USA	70	3.7	Killingbeck et al. 1990
Quercus alba‡	New York, USA	55	1.8	Woodwell 1974
Quercus coccinea‡	New York, USA	38	1.2	Woodwell 1974
Quercus ilicifolia	Rhode Island, USA	47	5.2	Killingbeck and Costigan 1988
Quercus ilicifolia‡,‖	Rhode Island, USA	37	2.6	May and Killingbeck 1992
Quercus macrocarpa	Kansas, USA	75	10.0	Killingbeck 1984
Quercus muhlenbergii	Kansas, USA	80	12.0	Killingbeck 1984
Ulmus rubra	Kansas, USA	95	11.0	Killingbeck 1984
Vaccinium vacillans	Rhode Island, USA	43	3.9	Killingbeck and Costigan 1988
Mean		66	5.0	
Standard error of the mean		7	0.8	

† Lowest N and P values among multiple sites.
‡ Interpolated from a figure in the citation.
§ Mean of high and low crown leaves.
‖ Lowest N and P values among multiple years.
¶ Genus known to be actinorhizal (nitrogen-fixing symbiont = *Frankia*).
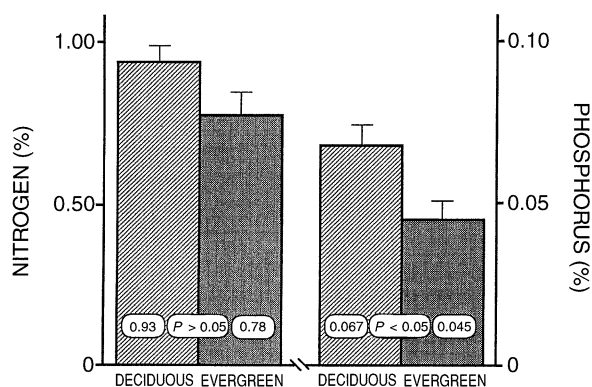

FIG. 1.   Mean concentrations (%) of nitrogen (N) and phosphorus (P) in the senesced leaves of 45 species of deciduous woody perennials and 32 species (N) or 31 species (P) of evergreen woody perennials. Error bars represent 1 SE, and probabilities (*P*) represent differences between deciduous and evergreen species based on Student's *t* test (for N) or the Kruskal-Wallis statistic (for P).

Wallis), subclasses within Anthophyta (Dilleniidae, Hamamelidae, and Rosidae: $P < 0.05$ for both N and P, ANOVA), and genera ($P < 0.05$ for N, ANOVA; $P < 0.05$ for P, Kruskal-Wallis). Conifers (Coniferophyta) produced senesced leaves with lower concentrations of N than did flowering plants (Anthophyta). N and P concentrations in the senesced leaves of the subclass Rosidae (*Acer, Eucalyptus*) were significantly lower than in senesced leaves of the subclass Hamamelidae (*Betula, Fagus, Quercus*; $P < 0.05$ for both N and P, Fisher's LSD test).

The genus *Eucalyptus* and the three genera within the Hamamelidae subclass occupied opposite ends of a continuum in senesced leaf N and P (Fig. 2). The senesced leaves of all three Hamamelidae genera held similar concentrations of N and P, but all contained significantly higher concentrations of N and P than did the leaves of *Eucalyptus* (Fisher's LSD test for N, Mann-Whitney *U* test for P). The senesced needles of *Larix* and *Pinus* held identical mean concentrations of N (0.59%), yet senesced *Larix* needles held higher concentrations of P (0.11%) than did *Pinus* needles (0.04%; Fig. 2).

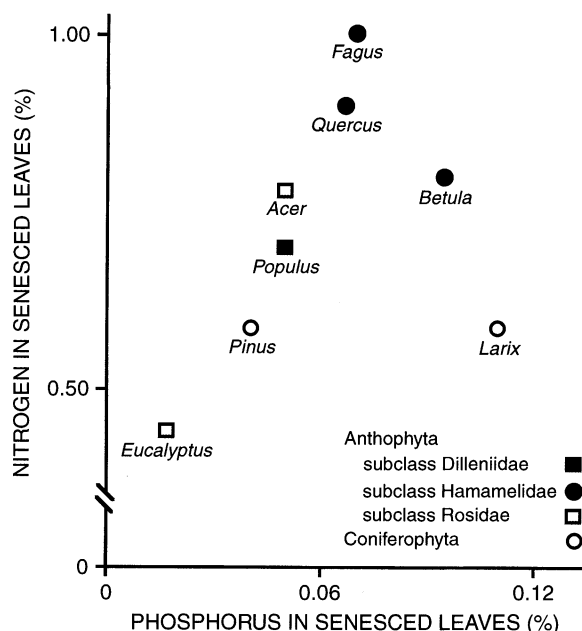Concentrations of N and P in the senesced leaves

FIG. 2. Mean concentrations (%) of N and P in the senesced leaves of eight genera. Symbols indicate genera within the same taxonomic subclass in Anthophyta, or within the same division in Coniferophyta. (n = 3, 4, 4, 3, 3, 4, and 15 for *Acer, Betula, Eucalyptus, Fagus, Larix, Populus,* and *Quercus,* respectively; n = 8 and 9 for phosphorus and nitrogen, respectively, in *Pinus*)

of congeners often varied widely (Table 1). Nitrogen ranged from 0.50–1.17% in congeners of *Betula,* 0.34–1.00% in congeners of *Pinus,* and 0.45–1.50% in congeners of *Quercus.* Phosphorus varied from four- to fivefold in congeners of *Betula, Populus,* and *Quercus.*

Six species were segregated into a separate table because of their potential access to internally fixed N (Table 2). All six are in genera known to be actinorhizal. Although that does not necessarily mean that the plants in question received N from *Frankia* symbionts, or even were nodulate, the high N found in the green leaves of four of these species suggests that at least these four were receiving fixed N from internal symbionts. Mean N concentration (1.61%) in the senesced leaves of potential N-fixers was significantly higher than in the senesced leaves of all other species (0.87%; P < 0.001, Student's t test). Only three of the 77 species in Table 1 (*Duguetia lucida, Sambucus nigra,* and *Symplocos ramosissima*) had N concentrations as high as the mean N concentration for the potential N-fixers. There was no statistically significant disparity in mean P concentrations between potential N-fixers and nonfixers (P > 0.05, Kruskal-Wallis).

Many studies of resorption are based on changes in

nutrient content per unit leaf area (micrograms per square centimetre), rather than on changes in nutrient concentration (%), to avoid potential problems of interpretation inherent in comparing concentrations between two or more points in time (see Guha and Mitchell 1966). Content of N in the senesced leaves of 22 species of woody perennials varied from 22 µg/cm² in *Hamamelis virginiana* growing in Ohio, to 142 µg/cm² in *Comptonia peregrina* growing in Rhode Island (Table 3). Mean N content was 66 µg/cm² for all 22 species, and 62 µg/cm² excluding *Comptonia peregrina,* the only actinorhizal species present in Table 3. Content of P varied from 0.3 µg/cm² in *Cyrilla racemiflora* growing in Georgia, to 12.0 µg/cm² in *Quercus muhlenbergii* growing in Kansas. Mean P content for all 22 species was 5.0 µg/cm².

Correlation coefficients decribing the relationship between N and P in senesced leaves proved to be consistently positive and significant. For all entries in Table 1 that included both N and P data, N and P concentrations were significantly correlated (r = 0.54; P < 0.01; n = 85). When deciduous and evergreen species were considered separately, N and P were more highly correlated in evergreen (r = 0.78; P < 0.01; n = 31) than in deciduous species (r = 0.45; P < 0.01; n = 54). N and P concentrations in the senesced leaves of actinorhizal species (Table 2) were also correlated (r = 0.89; P < 0.05; n = 5). Contents (micrograms per square centimetre) of N and P (Table 3) were also correlated, regardless of whether *Comptonia peregrina* was excluded (r = 0.64; P < 0.01; n = 22) or retained (r = 0.47; P < 0.05; n = 23).

Discussion

Potential resorption

Nitrogen and phosphorus levels in the senesced leaves of the 88 species used in this analysis are the result of a continuum of realized resorption. Year-to-year variation in the resorption of one or more nutrients is a constant feature of the few studies that have measured resorption in at least three successive years (Killingbeck et al. 1990, May and Killingbeck 1992, Killingbeck 1993a). Therefore, potential, maximum resorption must not be achieved in many years. Given the fact that most data presented in Tables 1–3 were the result of single-year measurements, it is clear that the range of values represents the gamut of resorption from incomplete realized resorption to maximum potential resorption.

Ultimate potential resorption of N and P, defined as the maximum levels to which these nutrients can be reduced in senescing leaves of any species, appeared to take place in five species of evergreens: *Banksia grandis,* two species of *Eucalyptus, Lyonia lucida,* and

Pinus rigida. These species reduced both N and P to lower concentrations in their senescing leaves (0.3% N, 0.01% P; Table 1) than did all other species. Ultimate potential resorption based on nutrient content per unit area of leaf is less definitive than that based on nutrient concentration, because of the relatively small data set (Table 3). Yet, based on N data for *Hamamelis virginiana* and P data for *Cyrilla racemiflora, Leucothoe racemosa, Lyonia lucida,* and *Quercus coccinea,* N and P can be reduced to ≈20 μg/cm² and 1.0 μg/cm², respectively. These nutrient levels, therefore, are the current best estimates of ultimate potential resorption for N and P, and probably define the biochemical limits to which N and P can be reduced in senescing leaves.

It is clear that plants producing senesced leaves with levels of nutrients substantially higher than the minima listed here have not fully conserved foliar nutrients. In other words, resorption is incomplete. One of the important features of knowing the levels to which N and P can be reduced in senescing leaves is that these values offer an objective gauge by which resorption can be measured, a gauge not subject to the vagaries of green-leaf nutrient content or timing of green-leaf sampling. For example, consider the differences in resorption efficiency reported for three populations of *Quercus alba* (Table 1). The Ohio (0.6% N) and New York (0.5% N) populations reduced N to half that of the Tennessee population (1.2% N); therefore, the first two populations were clearly more effective at reducing N in their senescing leaves. However, autumnal resorption efficiencies, reported as the percent reduction in N from green leaves, were 46%, 20%, and 36% for the Ohio, New York, and Tennessee populations, respectively. Based on this information alone, one would have to assume that resorption was nearly twice as successful in the Tennessee population as in the New York population when, in fact, the reverse was true.

Part of the resolution to this paradox may lie in the fact that some N was moved out of the New York *Quercus* leaves early in the growing season (Woodwell 1974), leaving relatively low N in green, late-summer leaves, and resulting in a diminished autumnal resorption efficiency value. However, this may also have occurred in the Tennessee population. Further, the comparison between the Ohio and Tennessee populations still creates an interpretational dilemma. By examining the concentration of N in the senesced leaves of these three *Quercus* populations, and knowing that potential resorption can reduce N to levels as low as 0.3%, it seems evident that the Tennessee *Quercus* population should have been able to withdraw much more N from its senescing leaves than it did,

thus making it physiologically much less effective than the other two *Quercus* populations at resorbing N.

Efficient vs. proficient resorption

The interpretational dilemma posed by the *Quercus alba* data points out the fundamental difference between viewing resorption in terms of percent reduction between green and senesced leaves (resorption efficiency) and terminal content in senesced leaves (resorption proficiency). Both are perfectly valid ways of looking at resorption, but the latter appears to be especially useful in addressing questions related to the evolution of the resorption process itself and to the selection pressures that have, and have not, influenced this process. For example, Scott et al. (1992) reported resorption efficiencies of 17–73% for N and 41–82% for P in six Brazilian rain forest species, and concluded that this wide range of values "suggests no strong selection for nutrient retranslocation [resorption]. . . ." On the contrary, all six species reduced P in their senescing leaves to virtually identical levels (0.04–0.06%; see *Brosimum lactescens, Duguetia lucida, Lecythis corrugata, Licania kunthiana, Pouteria hispida,* and *Tetragastris panamensis* in Table 1). Proficiency of P resorption was nearly identical, not disparate, thus supporting a conclusion opposite that proffered by Scott et al. (1992). Additionally, five of the six species retained high amounts of N in their senesced leaves (>1.0%), suggesting incomplete resorption. Without knowing what maximum, potential resorption is in these species, we have no way to judge whether or not these species differ in their evolved ability to reduce N in their senescing leaves.

A brief analysis of resorption dynamics in a guild of understory shrub species (Killingbeck and Costigan 1988) may further illustrate the magnitude of the difference between resorption efficiency and proficiency. Resorption efficiency varied from 26% to 70% for N, and from 28% to 59% for P among the three guild species (differences in efficiencies among species: $P < 0.001$ for N; $P < 0.05$ for P), suggesting a distinct species divergence in resorption ability. However, there were no differences in resorption proficiencies among the same species ($P > 0.05$; differences in N and P concentrations in senesced leaves among species). Analysis of efficiency suggested species divergence. Analysis of proficiency suggested species convergence.

These comparisons illustrate that efficiency and proficiency are different fundamental attributes of the same process. Both are ecologically important, but because they offer different insights into the evolution and functioning of the resorption process, how and when these measures of resorption should be used be-
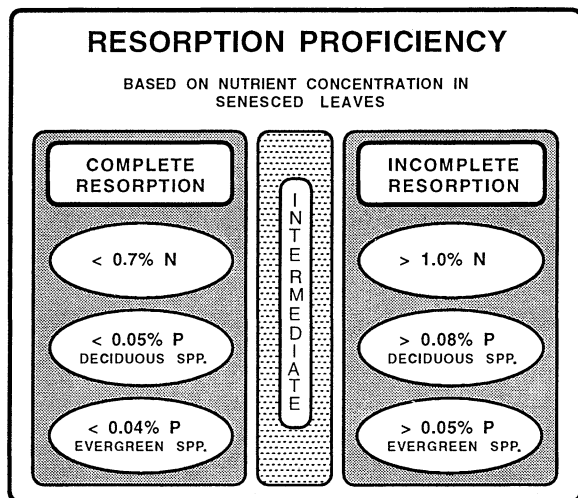
FIG. 3. Ranges of N and P concentrations (%) in senesced leaves representative of complete and incomplete resorption. Complete resorption is synonymous with high resorption proficiency, and incomplete resorption is synonymous with low resorption proficiency. P concentrations were segregated between deciduous and evergreen species because of the large difference between these two life-forms in ability to reduce P in senescing leaves (see Fig. 1).

FIG. 4. Ranges of N and P contents ($\mu g/cm^2$) in senesced leaves representative of complete and incomplete resorption. Complete resorption is synonymous with high resorption proficiency, and incomplete resorption is synonymous with low resorption proficiency.

comes a pertinent question. Efficiency values are best suited for resolving issues related to the *relative* degree to which individuals, populations, and communities can conserve nutrients invested in foliage so as to minimize subsequent uptake. The unique feature of efficiency as a measure of resorption is that it encompasses both nutrient demand (green-leaf nutrient content) and nutrient withdrawal.

Proficiency values, the *absolute* levels to which nutrients are reduced in senescing leaves, appear to be a more definitive and objective measure of the degree to which selection has acted to minimize nutrient loss. For example, selection for nutrient conservation would unquestionably be considered to have been stronger in a population that reduced N in its senescing leaves to 0.3% than in one that reduced N to 1.3%, even if their resorption efficiencies were identical. The assumption that resorption and fitness are linked is central to the validity of this example, and is supported by empirical evidence (May and Killingbeck 1992).

Regardless of the differences between resorption efficiency and proficiency, their complementary nature suggests that they may often be used most effectively in combination with one another.

Categories of resorption proficiency

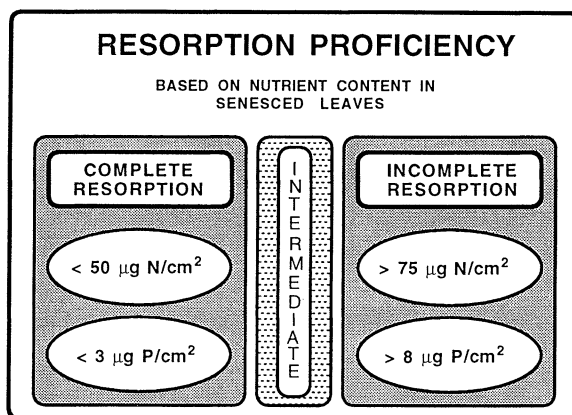It is not difficult to surmise that the lowest measured values of N and P in senesced leaves represent the end

point of potential resorption. What is difficult to determine is the range of values that adequately represents proficient, complete resorption for the majority of woody perennial species, since there is no basis for assuming that all species can reduce N and P to identical levels in their senescing leaves. A range of values must exist that encompasses the end point of potential resorption for many, if not the majority, of species. Likewise, a range of values must exist that portrays incomplete resorption for woody perennial species.

Based on patterns that emerged from the data on N and P in senesced leaves (Tables 1 and 3) and inferences from the literature about what may constitute proficient resorption, I offer two models that define and predict resorption proficiency in terms of concentration (Fig. 3) and content (Fig. 4) of N and P in senesced leaves. Thresholds of complete resorption are the concentrations or contents below which fall 35–45% of all resorption records cited in Tables 1 or 2. For example, 34 of 88 individual records (39%) in Table 1 fall below 0.7% N. The zone of intermediate resorption proficiency, located between complete and incomplete resorption, was determined as the next highest 25–30% of all records. This buffer zone is an acknowledgment of the uncertainty surrounding the categorization of complete vs. incomplete resorption. Finally, all values above the zone of intermediate resorption were considered to depict resorption that was incomplete.

The model based on terminal concentrations in senesced leaves includes a double set of boundaries for P, because of the substantial difference in P reductions between deciduous and evergreen species (Fig. 1). The

lack of a double set of P boundaries for the model based on nutrient content does not imply that such a division does not exist. It merely reflects the relative scarcity of resorption data based on content per unit leaf area. There will no doubt be the allure, and possibly the need, to tinker with the precise boundaries of the proficiency categories, but as they stand, the boundaries in these models generally appear to be consistent with our current understanding of resorption dynamics, and represent a viable first approximation of resorption proficiency.

Differences in resorption proficiency between deciduous and evergreen plants

Data on resorption efficiency have suggested that (1) evergreen species withdraw more nutrients from senescing leaves than do deciduous species (Gray 1983, Aerts 1990); (2) deciduous species withdraw more nutrients than do evergreen species (Tyrrell and Boerner 1987 [N only], del Arco et al. 1991, Son and Gower 1991); and (3) there is no difference in resorption between evergreen and deciduous species (Tyrrell and Boerner 1987 [P only], Pugnaire and Chapin 1993). The absence of a consistent trend in this debate may be the result of the confounding effects of variable stand conditions (Son and Gower 1991), but may also simply reflect the fact that short-term analyses of resorption efficiency are susceptible to year-to-year stochasticity in realized resorption, and do not directly consider terminal concentrations of nutrients in senesced leaves.

Analysis of N and P in senesced leaves indicates that evergreens and deciduous woody perennials do not differ in their abilities to reduce N in senescing leaves, but differ substantially in their abilities to reduce P (Fig. 1). Evergreens are more proficient at reducing P in their senescing leaves than are deciduous species. Implications of this finding include the speculation that evergreens may be able to colonize P-deficient sites more effectively than deciduous species. Regardless of such speculation, when proficiency is used as a direct measure of resorption, it is clear that evergreens are more effective than deciduous species at resorbing P.

The influence of phylogeny on resorption proficiency

Although resorption has been shown to be adaptive in the only species in which evolutionary fitness has been directly compared to resorption (*Quercus ilicifolia*; May and Killingbeck 1992), it is possible that certain trends in resorption proficiency are simply a function of phylogeny (T. Dawson, *personal communication*). Similarities in resorption among closely related taxa and dissimilarities among weakly related taxa would suggest the possibility of a phylogenetic influence on the process of resorption.

Significant similarities in N and P resorption proficiencies among related taxa and dissimilarities among distantly related taxa were evident in the analysis of the eight genera for which there were three or more observations in Table 1. Differences among taxonomic divisions, subclasses, and genera support the possibility of a phylogenetic influence. The tight clustering of the three genera in the subclass Hamamelidae was particularly striking, as was the dissimilarity between *Eucalyptus* and the other seven genera (Fig. 2).

Differences in resorption proficiency among congeners in Table 1, however, were so high (e.g., N in *Betula, Pinus,* and *Quercus*; P in *Betula, Populus,* and *Quercus*) as to suggest that phylogeny does not have an overriding impact on resorption. Further, the differences in P resorption proficiency between highly related genera such as *Larix* and *Pinus* serve as a glaring exception to the notion of strict phylogenetic control. Differences observed between *Eucalyptus* growing in Australia and other genera were probably a function of both phylogeny and environment, not just phylogeny. Although phylogeny and historical constraints (sensu Wanntorp 1983) appear to influence resorption proficiency, trends evident in this analysis suggest that the effects are not so significant as to overwhelm the effects of recent selection.

Resorption in species with and without N-fixing symbionts

Plants harboring N-fixing symbionts have consistently low N-resorption efficiencies (Stachurski and Zimka 1975, Dawson and Funk 1981, Rodriguez-Barrueco et al. 1984, Côté and Dawson 1986, Côté et al. 1989, Killingbeck 1993a). The level to which nitrogen can be reduced in the senescing leaves of potential N-fixers (1.61% N, Table 2) was almost twice that of nonfixers (0.87% N, Table 1), providing further support for the existence of an evolutionary trade-off between N fixation and effective resorption of N (Killingbeck 1993a). The fact that P resorption proficiency did not differ between N-fixers and nonfixers (Tables 1 and 3) also lends credence to the trade-off hypothesis.

The degree of relatedness between N and P in senesced leaves

The question of whether or not resorption patterns of different nutrients are related has been considered (e.g., Hill 1980, Chapin and Kedrowski 1983, Shaver and Melillo 1984, Killingbeck 1993a) but not resolved. A high degree of internutrient independence has been suggested by the absence of significant cor-

relations between N and P resorption efficiencies (Shaver and Melillo 1984, Killingbeck 1993a). However, the levels to which N and P were reduced in senescing leaves were significantly correlated in the present study. This linkage may suggest that, although the biochemical processes involved in mobilizing and transporting N and P out of leaves are to some degree independent of one another, selection for low terminal concentrations in senesced leaves is equally intense, or relaxed, for both elements in conspecific individuals growing in the same environment.

Conclusions

The most definitive, interpretable measure of resorption success may well be the level to which nutrients can be reduced in senescing leaves (resorption proficiency). Measurement and analysis of resorption proficiency, when coupled with a concurrent consideration of potential resorption, should facilitate the ongoing attempt to resolve complex questions regarding the environmental constraints that influence resorption in the short term, and the selection pressures that have directed the evolution of this process. Estimates of resorption efficiency (percent reduction from green leaves) have been, and will continue to be, important to our understanding of the resorption process. However, I suggest that a multifaceted approach may be most advantageous to the consideration of the resorption process, especially when questions of evolutionary selection are considered. Perhaps some of the dilemmas we have chased for decades can be more successfully resolved if we use the concepts of resorption efficiency, resorption proficiency, and potential resorption in concert.

Literature Cited

Aerts, R. 1990. Nutrient-use efficiency in evergreen and deciduous species from heathlands. Oecologia **84**:391–397.

Baker, D. D., and C. R. Schwintzer. 1990. Introduction. Pages 1–13 in C. R. Schwintzer and J. D. Tjepkema, editors. The biology of Frankia and actinorhizal plants. Academic Press, San Diego, California, USA.

Baker, J. B., and B. G. Blackmon. 1977. Biomass and nutrient accumulation in a cottonwood plantation—the first growing season. Journal of the Soil Science Society of America **41**:632–636.

Birk, E. M., and P. M. Vitousek. 1986. Nitrogen availability and nitrogen-use efficiency in loblolly pine stands. Ecology **67**:69–79.

Boerner, R. E. J. 1984. Foliar nutrient dynamics and nutrient-use efficiency of four deciduous tree species in relation to site fertility. Journal of Applied Ecology **21**:1029–1040.

———. 1985. Foliar nutrient dynamics, growth, and nutrient-use efficiency of Hamamelis virginiana in three forest microsites. Canadian Journal of Botany **63**:1476–1481.

Chapin, F. S., III. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics **11**:233–260.

Chapin, F. S., III, and R. A. Kedrowski. 1983. Seasonal changes in nitrogen and phosphorus fractions and autumnal retranslocation in evergreen and deciduous taiga trees. Ecology **64**:376–391.

Chapin, F. S., III, and L. Moilanen. 1991. Nutritional controls over nitrogen and phosphorus resorption from Alaskan birch leaves. Ecology **72**:709–715.

Côté, B., and J. O. Dawson. 1986. Autumnal changes in total nitrogen, salt-extractable proteins, and amino acids in leaves and adjacent bark of black alder, eastern cottonwood, and white basswood. Physiologica Plantarum **67**:102–108.

Côté, B., C. Vogel, and J. O. Dawson. 1989. Autumnal changes in tissue nitrogen of autumn olive, black alder, and eastern cottonwood. Plant and Soil **118**:23–32.

Cronquist, A. 1988. The evolution and classification of flowering plants. Second edition. New York Botanical Garden, Bronx, New York, New York, USA.

Dawson, J. O., and D. T. Funk. 1981. Seasonal change in foliar nitrogen concentration of Alnus glutinosa. Forest Science **27**:239–243.

del Arco, J. M., A. Escudero, and M. V. Garrido. 1991. Effects of site characteristics on nitrogen retranslocation from senescing leaves. Ecology **72**:701–708.

DeLucia, E. H., and W. H. Schlesinger. 1995. Photosynthetic rates and nutrient-use efficiency among evergreen and deciduous shrubs in Okefenokee Swamp. International Journal of Plant Sciences **156**:19–28.

Dierberg, F. E., P. A. Straub, and C. D. Hendry. 1986. Leaf-to-twig transfer conserves nitrogen and phosphorus in nutrient-poor and enriched cypress swamps. Forest Science **32**:900–913.

Escudero, A., J. M. del Arco, I. C. Sanz, and J. Ayala. 1992. Effects of leaf longevity and retranslocation efficiency on the retention time of nutrients in the leaf biomass of different woody species. Oecologia **90**:80–87.

Fries, N. 1952. Variations in the content of phosphorus, nucleic acids, and adenine in the leaves of some deciduous trees during the autumn. Plant and Soil **4**:29–42.

Gray, J. T. 1983. Nutrient use by evergreen and deciduous shrubs in southern California I. Community nutrient cycling and nutrient-use efficiency. Journal of Ecology **71**:21–41.

Grizzard, T., G. S. Henderson, E. E. C. Clebsch, and D. E. Reichle. 1976. Seasonal nutrient dynamics of foliage and litterfall on Walker Branch watershed, a deciduous forest ecosystem. Publication 814. Oak Ridge National Laboratory, Environmental Sciences Division, Oak Ridge, Tennessee, USA.

Guha, M. M., and R. L. Mitchell. 1966. The trace and major

element composition of the leaves of some deciduous trees II. Seasonal changes. Plant and Soil 24:90–112.

Hill, J. 1980. The remobilization of nutrients from leaves. Journal of Plant Nutrition 2:407–444.

Hocking, P. J. 1982. Effect of water stress on redistribution of nutrients from leaflets of narrow-leaved lupin (*Lupinus angustifolius* L.). Annals of Botany 49:541–543.

Hoyle, M. C. 1965. Variation in foliage composition and diameter growth of yellow birch with season, soil, and tree size. Proceedings of the Soil Science Society of America 29:475–480.

Jonasson, S. 1989. Implications of leaf longevity, leaf nutrient re-absorption, and translocation for the resource economy of five evergreen plant species. Oikos 56:121–131.

Killingbeck, K. T. 1984. Nitrogen and phosphorus resorption dynamics of five tree species in a Kansas gallery forest. American Midland Naturalist 111:155–164.

———. 1986. The terminological jungle revisited: making a case for use of the term resorption. Oikos 46:263–264.

———. 1992. Inefficient nitrogen resorption in a population of ocotillo (*Fouquieria splendens*), a drought-deciduous desert shrub. Southwestern Naturalist 37:35–42.

———. 1993a. Inefficient nitrogen resorption in genets of the actinorhizal nitrogen-fixing shrub *Comptonia peregrina*: physiological ineptitude or evolutionary trade-off? Oecologia 94:542–549.

———. 1993b. Nutrient resorption in desert shrubs. Revista Chilena de Historia Natural 66:345–355.

Killingbeck, K. T., and S. A. Costigan. 1988. Element resorption in a guild of understory shrub species: niche differentiation and resorption thresholds. Oikos 53:366–374.

Killingbeck, K. T., J. D. May, and S. Nyman. 1990. Foliar senescence in an aspen (*Populus tremuloides*) clone: the response of element resorption to interramet variation and timing of abscission. Canadian Journal of Forest Research 20:1156–1164.

May, J. D., and K. T. Killingbeck. 1992. Effects of preventing nutrient resorption on plant fitness and foliar nutrient dynamics. Ecology 73:1868–1878.

Miller, R. B. 1963. Plant nutrients in hard beech II. Seasonal variation in leaf composition. New Zealand Journal of Science 6:378–387.

Montes, R., and E. Medina. 1977. Seasonal changes in nutrient content of leaves of savanna trees with different ecological behavior. Geo-Eco-Tropica 4:295–307.

Näsholm, T. 1994. Removal of nitrogen during needle senescence in Scots pine (*Pinus sylvestris* L.). Oecologia 99:290–296.

O'Connell, A. M., T. S. Grove, and G. M. Dimmock. 1978. Nutrients in the litter of jarrah forest soils. Australian Journal of Ecology 3:253–260.

O'Connell, A. M., and P. M. A. Menagé. 1982. Litter fall and nutrient cycling in karri (*Eucalyptus diversicolor* F. Muell.) forest in relation to stand age. Australian Journal of Ecology 7:49–62.

O'Neill, R. V., and D. L. DeAngelis. 1981. Comparative productivity and biomass relations of forest ecosystems. Pages 411–449 *in* D. E. Reichle, editor. Dynamic properties of forest ecosystems. Cambridge University Press, Cambridge, England.

Olsen, C. 1948. The mineral, nitrogen, and sugar content of beech leaves and beech leaf sap at various times. Comptes Rendus des Travaux du Laboratoire Carlsberg Serie Chimique 26:197–230.

Polglase, P. J., and P. M. Attiwill. 1992. Nitrogen and phosphorus cycling in relation to stand age of *Eucalyptus regnans* F. Muell. Plant and Soil 142:157–166.

Pugnaire, F. I., and F. S. Chapin, III. 1993. Controls over nutrient resorption from leaves of evergreen Mediterranean species. Ecology 74:124–129.

Ralhan, P. K., and S. P. Singh. 1987. Dynamics of nutrients and leaf mass in central Himalayan forest trees and shrubs. Ecology 68:1974–1983.

Rodriguez-Barrueco, C., C. Miguel, and P. Subramaniam. 1984. Seasonal fluctuations of the mineral concentration of alder (*Alnus glutinosa* (L.) Gaertn.) from the field. Plant and Soil 78:201–208.

Scott, D. A., J. Proctor, and J. Thompson. 1992. Ecological studies on a lowland evergreen rain forest on Maraca Island, Brazil II. Litter and nutrient cycling. Journal of Ecology 80:705–717.

Shaver, G. R., and J. M. Melillo. 1984. Nutrient budgets of marsh plants: efficiency concepts and relation to availability. Ecology 65:1491–1510.

Small, E. 1972. Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog plants. Canadian Journal of Botany 50:2227–2233.

Son, Y., and S. T. Gower. 1991. Aboveground nitrogen and phosphorus use by five plantation-grown trees with different leaf longevities. Biogeochemistry 14:167–191.

Staaf, H. 1982. Plant nutrient changes in beech leaves during senescence as influenced by site characteristics. Acta Ecologica 3:161–170.

Staaf, H., and I. Stjernquist. 1986. Seasonal dynamics, especially autumnal retranslocation, of nitrogen and phosphorus in foliage of dominant and suppressed trees of beech, *Fagus sylvatica*. Scandinavian Journal of Forest Research 1:333–342.

Stachurski, A., and J. Zimka. 1975. Methods of studying forest ecosystems: leaf area, leaf production, and withdrawal of nutrients from leaves of trees. Ekologia Polska 23:637–648.

Tilton, D. L. 1977. Seasonal growth and foliar nutrients of *Larix laricina* in three wetland ecosystems. Canadian Journal of Botany 55:1291–1298.

Turner, J., and P. R. Olson. 1976. Nitrogen relations in a Douglas-fir plantation. Annals of Botany 40:1185–1193.

Tyrrell, L. E., and R. E. J. Boerner. 1987. *Larix laricina* and *Picea mariana*: relationships among leaf life-span, foliar nutrient patterns, nutrient conservation, and growth efficiency. Canadian Journal of Botany 65:1570–1577.

Verry, E. S., and D. R. Timmons. 1976. Elements in leaves of a trembling aspen clone by crown position and season. Canadian Journal of Forest Research 6:436–440.

Wanntorp, H-E. 1983. Historical constraints in adaptation theory: traits and non-traits. Oikos 41:157–160.

Wilkinson, L. 1992. SYSTAT for the Macintosh, Version 5.2. SYSTAT, Evanston, Illinois, USA.

Woodwell, G. M. 1974. Variations in the nutrient content of leaves of *Quercus alba, Quercus coccinea,* and *Pinus rigida* in the Brookhaven Forest from bud-break to abscission. American Journal of Botany 61:749–753.